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Research Article

The fellowship of the fig continues its journey: Fig wasps (Hymenoptera, Chalcidoidea) associated with *Ficus microcarpa* in Greece

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Abstract

The number of alien species continues to climb uninterrupted with a proportion of them becoming invasive, impacting native biodiversity and socioeconomic parameters. Many alien species are plants, transported outside their native range, sometimes alongside their associated insects hitching a ride to new destinations. *Ficus microcarpa* L. (Moraceae) is a common ornamental plant in the Mediterranean, which has been found to host a large ecological network of associated chalcid wasps (also called fig wasps). Amongst them, the plant's pollinator *Eupristina verticillata* Waterston (Agaonidae), enhances the plant's successful pollination and subsequent germination, thus allowing it to establish viable populations and even become invasive in some parts of the world. Other associated wasps, also called non-pollinating fig wasps, have likewise followed and these are parasitoids, inquilines or gallers. These species can be either beneficial or injurious to *F. microcarpa*, with some even proposed as potential biological control agents mitigating the plant's spread. Seven fig wasp species have been reported from Greece, hitherto. Here, we present the first national survey of fig wasp fauna for Greece. We found 13 species, with six representing new records for the country (*Eufroggattisca okinavensis* Ishii, *Micranisa degastris* Chen, *Philotrypesis okinavensis* Ishii, *Philotrypesis taiwanensis* Chen, *Odontofroggatia quinifuniculus* Feng & Huang, *Sycophila curta* Chen) and two (*O. quinifuniculus*, *S. curta*) being reported outside their native range for the first time. *Philotrypesis emeryi* is removed from previous checklists upon molecular characterization of specimens as being *Philotrypesis okinavensis*. We discuss the distribution, introduction period and ecology of these fig wasps. Further, we present records of seedlings for *F. microcarpa* and discuss the potential implications of the fig wasp fauna for the establishment and control of this alien plant species.

Key words: Alien species, biological invasions, chalcid wasps, distribution, first records, ecological networks

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Introduction

International trade, along with globalisation and the constant transportation of people and goods around the world have greatly contributed to a rising number of species managing to reach areas beyond their natural distribution, a trend that continues uninterrupted (Hulme 2009; Seebens et al. 2017; Seebens 2019). A considerable number of these "alien" species have managed to establish viable populations and even become invasive in their newly-invaded areas (Wang 2014). Alien species can also trigger a series of adverse impacts on native biodiversity and ecosystem functions, human health and societal welfare, as well as negatively affecting global economy (Vilà and Hulme 2016; Mazza and Tricarico 2018; Haubrock et al. 2021). Biodiversity loss and pressures on native species by invasive alien species are evident *inter alia* through their competition with native and/or endemic species, alteration of trophic webs and transmissions of pathogens (Seebens et al. 2017; Chinchio et al. 2020). From a socioeconomic perspective, invasive alien species and their impacts have been thoroughly discussed in both the EU and the US (Pimentel et al. 2005; Kettunen et al. 2009; Haubrock et al. 2021).

Plant species have often been deliberately introduced in areas beyond their natural distribution for forestry, agricultural, medicinal or ornamental purposes, while there are also plenty of cases of unintentional introduction (Newsome and Noble 1986; Williamson 1996; Arianoutsou et al. 2010). The Mediterranean climate is suitable for the establishment of numerous alien plant species from tropical and sub-tropical as well as temperate areas (Bella 2014a) and their use as ornamentals in parks and gardens in Europe is increasing (Lopez-Vaamonde et al. 2010; Bella 2014b). Following on from introduction of their hosts, numerous insect species associated with introduced ornamentals have established in introduced areas (Bonnamour et al. 2023) where they are most commonly found in gardens and parks as well as other anthropogenic habitats (Lopez-Vaamonde et al. 2010). This broad trend is evident in Greece, as plant species such as *Eucalyptus* spp. have been associated with the unintentional introduction and establishment of various phytophagous chalcid wasps (including, but not limited to *Leptocybe invasa* Fischer & La Salle, 2004, *Ophelimus maskelli* Ashmead, 1900 and *Quadrastichodella nova* Girault, 1922) (Georgevits 1981; Kavallieratos et al. 2004; Anagnou-Veroniki et al. 2008).

The genus *Ficus* L. (Rosales, Moraceae) includes more than 800 species and is of remarkable ecological value, providing food or nesting sites to many vertebrates (Berg 1989; Shanahan et al. 2001; Wang 2014). The majority of *Ficus* species are distributed in Indomalaya, while around 150 species originate from each of the Afrotropics and the Neotropics (van Noort and Rasplus 2022). Fig tree fruits, known as "figs", are in fact an enclosed inflorescence, with numerous small flowers and are also termed "syconia" (Cook and Rasplus 2003). Figs can be viewed as a microhabitat for insect species that can be considered either as beneficial or injurious to the plant, depending on their trophic regime (Grandi 1961; Galil and Eisikowitch 1968b). Pollination of each *Ficus* species is carried out by species in the family Agaonidae (Hymenoptera, Chalcidoidea) and, in turn, these wasps depend on their host tree since they dwell and feed inside the figs (Galil and Eisikowitch 1968b; Cook and Rasplus 2003). This positive association known as a mutualism, is exploited by a series of non-pollinating species (Non-Pollinating Fig Wasps; NPFWs) of various trophic regimes (gallers, inquilines and parasitoids) (Chen et al. 1999; Cook and Rasplus 2003). Each *Ficus* species can host up to 30 species of

fig wasps or more, providing us with micro-community ecological models of great interest (Compton et al. 1994; West et al. 1996; Cook and Rasplus 2003).

Known by various common names (Chinese/Malayan Banyan or Cuban/Indian Laurel), *Ficus microcarpa* L. is a monecious fig tree species, originating from sub-tropical and tropical areas of south-eastern Asia (Chen et al. 1999; Wagner et al. 1999; Bhandari and Cheng 2016). The same species can also be found in literature under the synonyms *F. nitida* Thunberg and *F. retusa* L. (Mifsud et al. 2012). Mature individuals can have 4–5 crops per year (Chen et al. 1999), but less in seasonal climates. This species has been introduced as an ornamental in various tropical and subtropical areas of the world and, in the Mediterranean, it is common throughout parks, private gardens and road sideways (Wang et al. 2015b; Demetriou et al. 2023). In introduced areas, it can occasionally be the cause of damage to infrastructure, especially old buildings and even expand into natural habitats as an invasive species (Ramírez and Montero 1988; McKey 1989; Beardsley 1998; Tsintides et al. 2002; Mifsud 2014; Wang et al. 2015b; Demetriou et al. 2023).

Phytophagous insect species associated with *F. microcarpa* can be divided into two main subcategories, depending on the parts of the tree they exploit. Along with some other insects, a paraphyletic group of wasps of the superfamily Chalcidoidea are called fig wasps and are associated with the figs. Elsewhere on the tree, insects feed on the leaves, twigs and branches. They belong to various insect orders (Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, Thysanoptera) (van Noort and Rasplus 2022) and include some fig wasps that have apparently switched from galling figs to galling leaves and stems. Amongst these, described from outside its putative native range, *Josephiella microcarpae* Beardsley & Rasplus, 2001, has managed to spread throughout the Mediterranean and has been recently discovered from Greece (Crete, Rhodes) (Beardsley and Rasplus 2001; Kalaentzis et al. 2023; EK unpublished data). Other species, such as *Gynaikothrips ficorum* (Marchal, 1908) (Thysanoptera, Phlaeothripidae) along with its predator *Montandoniolla moraguesi* (Puton, 1896) (Hemiptera, Anthocoridae) and *Macrohomotoma gladiata* Kuwayama, 1908 have also managed to follow their host plant as pests and expand their distribution throughout southern Greece (Antonatos et al. 2015; Malumphy and Guillem 2020; EK, unpublished data). In turn, some of these fig tree pests have also been followed by their parasitoids, such as *Psyllaephagus macrohomotoma* Singh & Agarwal, 1993 and *Psyllaephagus schauffi* Japoshvili, 2023 (both parasitising *M. gladiata* in Greece and/or Cyprus) (Japoshvili et al. 2023).

Fig wasps can be further divided into trophic categories: those whose larvae feed on plant tissue inside galled ovules (phytophagous species) and those that fulfil their larval development at the expense of the phytophagous species (parasitoids, inquilines, secondary gallers and even hyper-parasitoids) (Compton et al. 2009; Segar and Cook 2012; Chen et al. 2013; Wang et al. 2015a). The most prominent phytophagous species is one of the pollinators of *F. microcarpa*, *Eupristina verticillata* Waterston 1921, which assists its host plant's reproduction by allowing it to produce fertile seeds in ripe figs, which, in turn, are carried away with the help of birds or even ants (Kaufmann et al. 1991). As a result, *F. microcarpa* has managed to escape urban habitats and, alongside its pollinator, it has a presence in all biogeographic regions, except for Antarctica (Wang et al. 2015a). Other fig wasps that inhabit the figs belong to families Epichrysomallidae, Eurytomidae, Ormyridae and Pteromalidae (Wang et al. 2015a; Burks et al. 2022). They exploit the mutualism between fig trees and their pollinator and undermine the reproductive success of their host plant

by reducing pollen dispersal and destroying ovules and seeds (Suleman et al. 2013; van Noort et al. 2013). As with the pollinator, many of these species display sexual dimorphism where females have fully developed eyes and wings in order to disperse in search of new host plants, whereas their males are often wingless, with smaller eyes and dwell their entire live inside the fig (Weiblen 2002; Zhou et al. 2012).

Following the description of the pollinator *E. verticillata* (Waterston, 1921), Ishii (1934) described six non-pollinating fig wasps from Japan. Years later, extended surveys of ornamental individuals of *F. microcarpa* from Florida revealed that four fig wasp species had managed to follow their host plant outside their native range for the first time (Nadel et al. 1992). Chen et al. (1999) described ten additional species from Taiwan and finally Wang et al. (2015a) created a list of a total of 32 morphospecies and species associated with *F. microcarpa*. Recently, Demetriou et al. (2023) reported eleven fig wasp species from the island of Cyprus, even reporting on finding a presumably new undescribed species belonging to Epichrysomallidae. Regarding Greece, Compton (1989) reported *Odontofroggatia galili* Wiebes, 1980 from the island of Symi as the first introduced fig wasp species in Europe. Material samplings from Rhodes and Symi nearly three decades after, revealed a total of seven alien fig wasp species (Wang et al. 2015a), suggesting that new species have been colonising rapidly in the intervening years. To date, no structured survey has been ever carried out at a mainland country level regarding the wasp fauna of *F. microcarpa*. Herein, we present the first detailed study on the fig wasp species related to *F. microcarpa* in Greece reporting on a total of 13 associated species.

Materials and methods

The only publications dealing with the fig wasp fauna of Greece are limited to Compton (1989), Wang et al. (2015a) and Wang et al. (2015b), where sampling was mainly restricted to the south-eastern Aegean islands of Rhodes and Symi. In order to bridge the knowledge gap, sampling was carried out throughout Greece, with an emphasis on its southern part, where *F. microcarpa* is more widespread. Since distributional records for *F. microcarpa* were not found in the scientific literature [except for Galanos (2015) - reporting for the first time on spontaneous plants near parent plants in urban areas of Rhodes], before visiting areas where host trees might be present, Google Maps, Google Street view, social media and citizen-science platforms (such as iNaturalist) were utilised. Starting in early 2021, samples were obtained in Attica (Att), Central Greece (CG), Crete (Cr), Cyclades (Cy), Dodecanese (Do), Ionian islands (Iis) and Peloponnese (Pel) (Fig. 1, Table 2, Suppl. material 2).

Monoecious figs development follows a series of five phases (A-E), with pollinators laying their eggs at B-phase, developing during C-phase and emerging during D-phase, while NPFW mainly oviposit during B or C-phase (a very few oviposit at A phase) and their offspring emerge at the same time with those of the pollinator (Galil and Eisikowitch 1968a; Wang et al. 2015a). As such, upon locating the fig tree crops, figs in late C to early D phase were collected, since these stages are optimal for obtaining adult wasps (Galil and Eisikowitch 1968a; Wang 2014; Wang et al. 2015a). During each collecting event, figs were put in sealed polyethylene bags and subsequently stored in 90° ethanol. Following Wang et al. (2015a), after removed from ethanol, collected figs were put in plastic boxes filled with water for 10 minutes and each fig was divided into four parts for further examination.

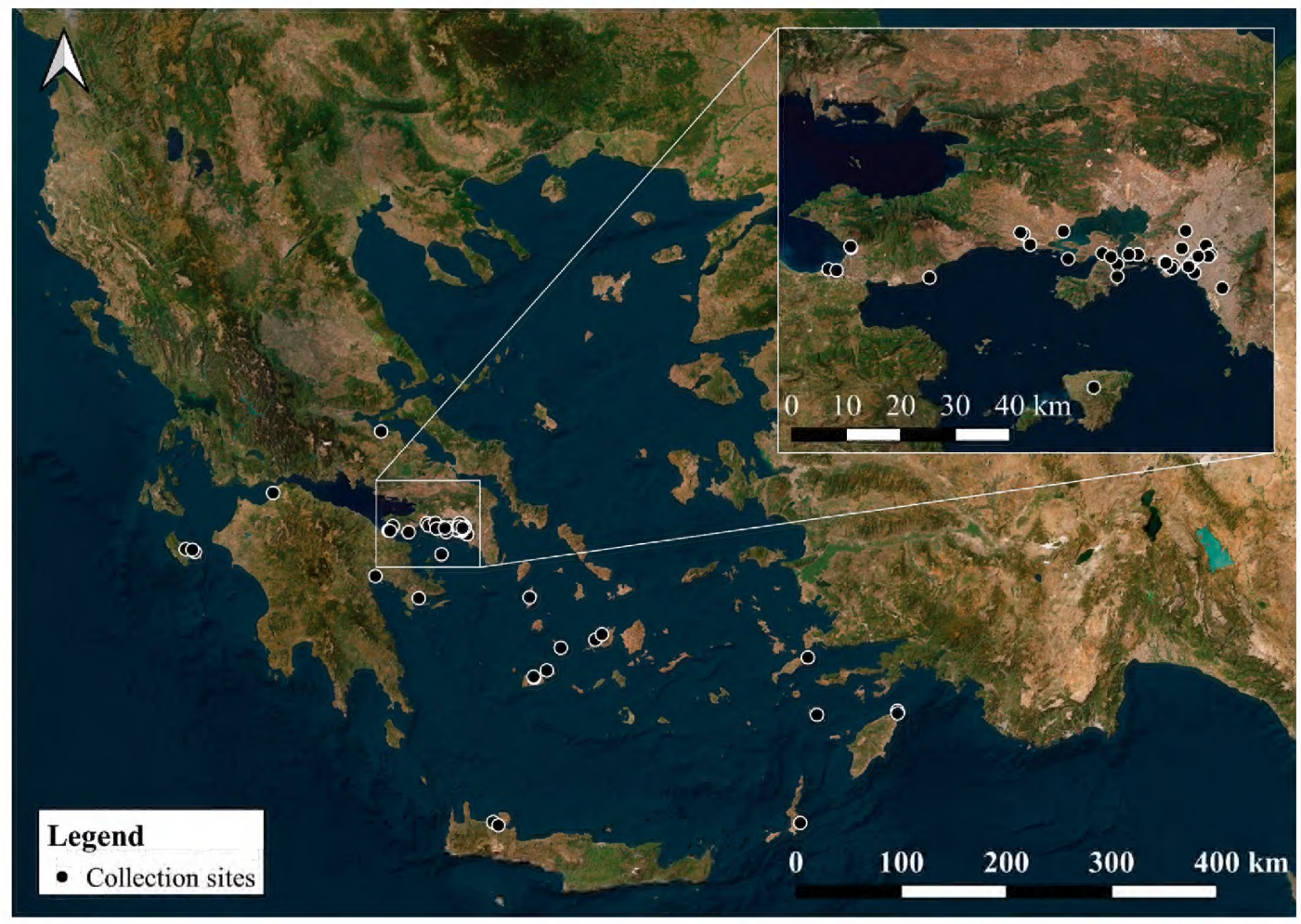

Figure 1. Collections of *Ficus microcarpa* figs.

Specimen rearing, storage and identification

Reared fig wasps that emerged before the figs' storage, were stored in 70° and 90° ethanol, for identification under a stereomicroscope and molecular treatment. A total of 7,292 figs from 58 localities were collected for this study. Dissected figs were observed under a stereomicroscope and observed galls were carefully opened with entomological forceps for the extraction of the wasps. In a similar manner, extracted samples were put in ethanol for future morphological or molecular examination. Specimens used for identification were either air-dried or dried using hexamethyldisilazane (HMDS) (Heraty and Hawks 1998) and mounted on rectangular paper cards. Identification was carried out following a combination of keys and descriptions (Ishii 1934; Beardsley 1998; Chen et al. 1999; Feng and Huang 2010; Ma et al. 2013; Wang et al. 2016; Xiao et al. 2021; van Noort and Rasplus 2022; Burks et al. 2022).

Molecular analysis

To ensure that all specimens are unambiguously assigned to a particular *Philotrypesis* species, besides using traditional morphological features, we also performed a molecular identification. After the PCR amplification of a fragment of the mitochondrial DNA (mtDNA) gene of Cytochrome c Oxidase Subunit I (COX1), the generated sequences, together with all available congeneric COX1 sequences available in GenBank, were analysed within a phylogenetic framework aiming to assess the relationship of the specimens of this study to the other *Philotrypesis* species.

DNA extraction and PCR amplification

Total genomic DNA from *Philotrypesis* individuals preserved in 100% ethanol was extracted using the CTAB (hexadecyl-trimethyl-ammonium bromide) protocol, as described in Parmakelis et al. (2005). In total, we extracted the DNA from 24

specimens. The whole body of the individuals was used in the extraction. However, specimens belonging to the same series with specimens used for DNA extraction were dried with HMDS and card mounted, allowing future morphological comparisons. PCR was carried out to amplify a fragment of the mitochondrial gene COX1 using the primer pair mt6 (C1-J-1718) and Nancy (C1-N-2191) (Simon et al. 1994). The total reaction volume was 25 μl, where 2 μl of template DNA was mixed with 0.2 mM dNTP's, 0.4 μM of each primer and 0.5 units of Taq polymerase and 3.5 mM $MgCl_2$. The reaction consisted of an initial denaturation step of 95 °C for 3 min, followed by 39 cycles of 15 sec at 94 °C, 1 min at 40 °C and 1.5 min at 72 °C. The cycling ended with a 10 min extension step at 72 °C. The PCR products were purified using the NucleoSpin Gel and PCR Clean-Up Kit (Macherey-Nagel). The purified PCR products were sequenced using the BigDye™ Terminator v.3.1 Cycle Sequencing Kit, utilising an automated sequencer at the CeMIA sequencing facility (CEMIA S.A., Greece). Both strands were sequenced and the primers used in the sequencing reactions were the same as in the amplification steps. Sequences were deposited in GenBank under the accession numbers PQ897148, PQ897149, PQ897150, PQ897151, PQ897152, PQ897153, PQ897154, PQ897155, PQ897156, PQ897157, PQ897158, PQ897159, PQ897160, PQ897161, PQ897162, PQ897163, PQ897164 and PQ897165.

Phylogenetic analysis

Along with the 18 sequences generated within this study, in the phylogenetic analysis, we used 276 COX1 sequences of *Philotrypesis* species that were available in GenBank. In addition, we used sequences of *Sycoscapter* spp. and *Walkerella microcarpae* Bouček, 1993 as outgroup taxa. Details of the origin of specimens used in the study and the accession numbers of sequences retrieved from GenBank are provided on Suppl. material 1. The generated *Philotrypesis* sequences were edited using CodonCode Aligner v. 9.0.1. The same software was used in the alignment of the sequences used in the phylogenetic analysis. Prior to the phylogenetic analysis, we used IQ-TREE v. 2.2.0 (Minh et al. 2020) in order to evaluate the best fitting nucleotide substitution model for the data at hand. The Bayesian Information Criterion (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017) was used to identify the best fitting model. The model selected and applied in the analysis was the GTR+I+G. MrBayes v. 3.2.7 (Ronquist and Huelsenbeck 2003) was used to perform Bayesian Inference analysis (BI). We set the parameters and priors, based on the substitution model implemented. The number of generations was set to 2×10^6 and two independent runs with four chains were performed. A consensus tree was constructed after discarding 25% of the generated trees as burn-in.

Results

Molecular and morphological identification of *Philotrypesis* specimens

The results of the phylogenetic analysis performed are presented in Fig. 2. It can be seen that all currently known *Philotrypesis* species for which available data existed in GenBank, were recovered as monophyletic groups. An exception to this is the species *Philotrypesis emeryi* Grandi, 1926, for which the respective sequences did

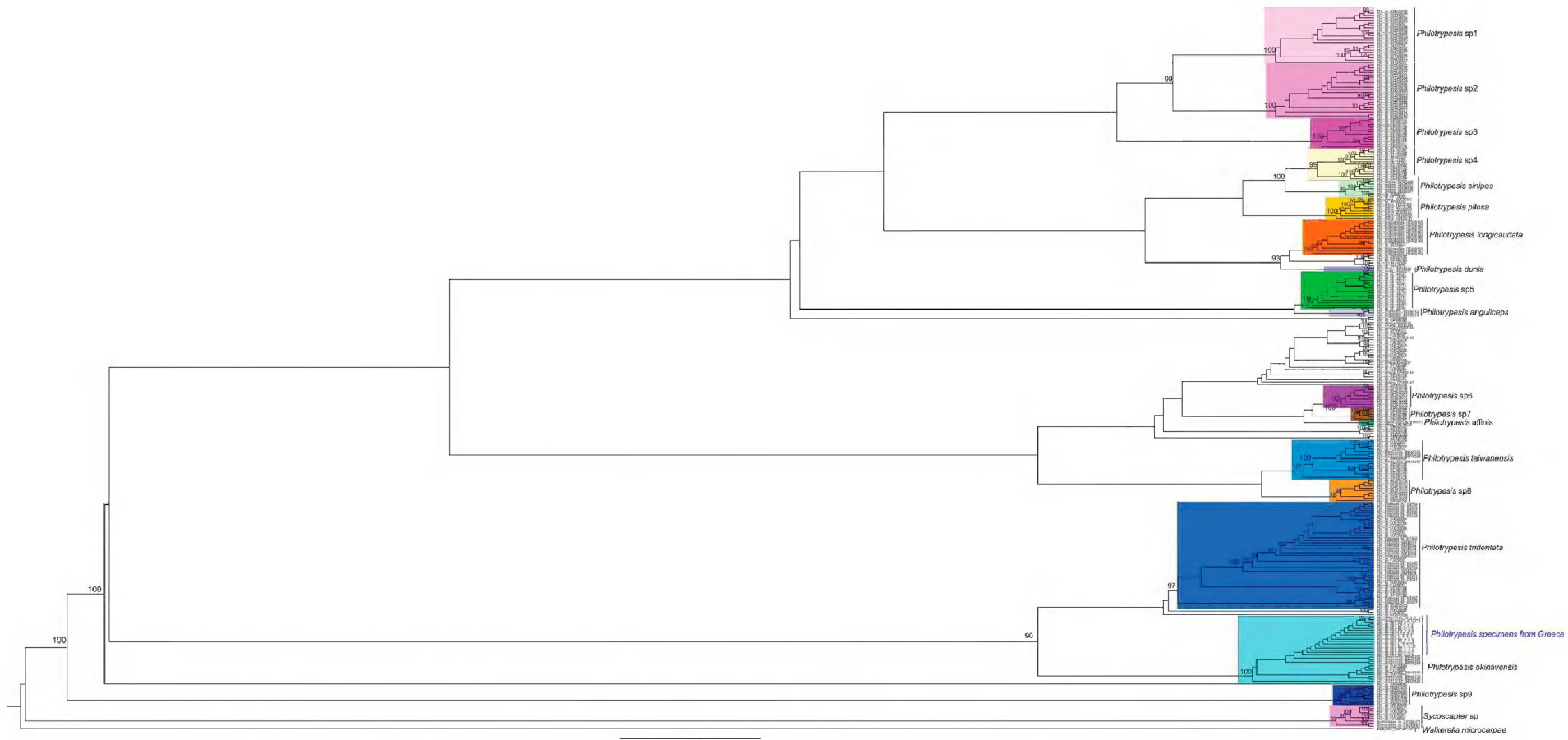

Figure 2. 50% majority rule consensus tree of the Bayesian Inference (BI) analysis. Values at nodes indicate the posterior probability (percent values) support of nodes. Only values above 90% are shown. *Philotrypesis* species for which sequence data were available in GenBank are indicated. Clades not corresponding to known *Philotrypesis* species are marked as sp1, sp2 etc. The specimens of *Philotrypesis* originating from Greece are indicated with the vertical blue bar.

not form a single clade. This could be due to several reasons. Misidentification of specimens deposited in GenBank is only one of them. However, the phylogenetic results point to the need for a taxonomic revision for this species. At this point, it should be mentioned that there are many cases where monophyletic groups are formed by several unassigned *Philotrypesis* lineages. This is typical in cases where cryptic speciation is present amongst morphologically indistinguishable species.

Regarding the affinity of the *Philotrypesis* specimens of this study, it seems that they are firmly placed within the *P. okinavensis* lineage (*sensu* Zhou et al. (2012)) that forms a well-supported monophyletic group. Especially regarding the specimens from Rhodes, they are clearly phylogenetically distinct from all instances of *P. emeryi* appearing on the tree. Although *P. emeryi* was first reported from both Rhodes and Symi (Wang et al. 2015a), morphological and molecular examination of our specimens from the island of Rhodes (Suppl. material 1) allowed us to exclude it from this list. Therefore, the reports of this species in Wang et al. (2015a) are misidentifications of *Philotrypesis okinavensis* Ishii, 1934.

The revised checklist of fig wasps associated with *F. microcarpa* in Greece includes thirteen (13) species, distributed in five families (Table 1, Figs 4, 5). A total of six species are reported for the first time from Greece: (i.e. *Eufroggattisca okinavensis*, *Micranisa degastris*, *Odontofroggatia quinifuniculus*, *Philotrypesis okinavensis*, *Philotrypesis taiwanensis*, *Sycophila curta*) and two of them (i.e. *O. quinifuniculus*, *S. curta*) are recorded outside their native range for the first time.

Species occurrence/frequency data

A total of 21457 fig wasps were sampled within this survey. Amongst the collected fig wasp species, *E. verticillata* was the most abundant (11.537 individuals), followed by *O. galili* (3.827), *M. bicolor* (1.840) and *W. microcarpae* (1.687) (Tables 2, 3). The pollinator was also widely distributed (82.7% prevalence), followed by

Table 1. Updated checklist of fig wasps associated with *F. microcarpa* in Greece, including their trophic regime.

No	Family	Subfamily	Species	Abbreviation	Trophic regime	Reference
1	Agaonidae	Agaoninae	*Eupristina verticillata* Waterston,1921	EV	ovule galler	Wang et al. (2015a)
2	Epichrysomallidae		*Eufroggattisca okinavensis* Ishii, 1934	EO	unknown	Present study
3			*Meselatus bicolor* Chen, 1999	MB	ovule galler	Wang et al. (2015a)
4			*Odontofroggatia galili* Wiebes, 1980	OG	ovule galler	Compton (1989)
5			*Odontofroggatia ishii* Wiebes, 1980	OI	ovule galler	Wang et al. (2015a)
6			*Odontofroggatia quinifuniculus* Feng & Huang, 2010	OQ	ovule galler	Present study
7	Eurytomidae	Eurytominae	*Sycophila curta* Chen, 1999	SC	parasitoid	Present study
8			*Sycophila maculafacies* Chen, 1999	SM	parasitoid	Wang et al. (2015a)
9	Ormyridae		*Ormyrus microcarpae* Askew & Koutsoukos, 2024	OR	parasitoid	Koutsoukos et al. (2024)
10	Pteromalidae	Pteromalinae	*Micranisa degastris* Chen, 1999	MD	ovule galler	Present study
11			*Philotrypesis okinavensis* Ishii, 1934	PO	parasitoid	Wang et al. (2015a)
12			*Philotrypesis taiwanensis* Chen, 1999	PT	seed eater	Present study
13			*Walkerella microcarpae* Bouček, 1993	WM	ovule galler	Wang et al. (2015a)

the phytophagous gallers *O. galili* (70.6%), *W. microcarpae* (70.6%) and *O. ishii* (43.1%) (Suppl. material 3). The most species-rich collection sites were located within Attica, Peloponnese and South Aegean (Cyclades and Dodecanese Islands) areas (10 species), followed by Crete (7 species). The most widely distributed species were *O. galili* (7 administrative divisions), followed by the pollinator *E. verticillata* (6 administrative divisions) and *M. bicolor*, *O. ishii* and *W. microcarpae* (5 administrative divisions) (Tables 2, 3).

Amongst the three time-intervals, one species was reported in 1989, six more in 2014 and seven more again during the last few years (Koutsoukos et al. 2024; present study). Regarding the ecology and trophic regimes of alien fig wasps, eight out of the thirteen collected species are phytophagous ovule gallers (including *E. verticillata*), while one is a seed eater (*P. taiwanensis*). The remaining four species are parasitoids. Namely, *Sycophila* spp. are parasitoids of *Odontofroggatia* spp., *P. okinavensis* is a parasitoid of *W. microcarpae*, while *Ormyrus microcarpae* is most likely a parasitoid of *M. bicolor* (Wang et al. 2015a; Koutsoukos et al. 2024).

Discussion

Distribution, abundance and diversity

We have presented the first survey of fig wasps associated with *F. microcarpa* at a country level in Greece. With six species presented as new records for the country, the fig wasp fauna has almost doubled since Compton (1989) and Wang et al. (2015a), currently including 13 alien species. At least 38 species are known to be associated with *F. microcarpa* in its native and introduced ranges, of which 16 have been reported outside their native range at least once, while the rest, to our knowledge, are restricted to their natural distribution (van Noort and Rasplus 2010; Li et al. 2013; Wang 2014; Wang et al. 2015a; van Noort and Rasplus 2022; Demetriou et al. 2023). Amongst the species collected, *O. quinifuniculus*, and *S. curta* were found outside their natural distribution for the first time. Interestingly, *O. microcarpae* was recently detected and described from Greece and Cyprus (Koutsoukos et al. 2024) and its precise native range remains unknown.

Table 2. Sampled localities and their species composition.

Adm. division	Site	Coordinates	Date(s)	Number of crops	Number of figs	Species present
ATT	Argiroupoli	37°54'32.4"N, 23°45'03.6"E	22.x.2021	1	23	OG, WM, EV, MB, SM
ATT	Athens Centre	37°58'45.7"N, 23°42'48.3"E	vii.2021	3	20	OG, EV
ATT	Egaleo, PADA	38°00'15.1"N, 23°40'32.9"E	iv-ix.2021	16	392	OG, OI, OQ, WM, PO, EV, MB, OR, SM, SC
ATT	Egina, Agios Nektarios	37°44'49.7"N, 23°29'01.5"E	7.xii.2021	1	37	OG, PO, EV
ATT	Faliro, Delta	37°56'03.6"N, 23°41'37.1"E	iv.-ix.2021	2	351	OG, OI, WM, EV, MB, SM, SC
ATT	Kallithea, Ilissos	37°56'58.7"N, 23°41'10.4"E	28.viii.2021	1	10	EV
ATT	Kallithea, Park 1	37°57'30.7"N, 23°41'48.0"E	28.viii.2021	1	17	OG, WM, EV
ATT	Kallithea, Park 2	37°57'41.0"N, 23°42'07.1"E	28.viii.2021	1	72	OG, WM, EV
ATT	Megara	37°59'46.0"N, 23°20'40.1"E	v-xi.2021	4	27	OG, EV
ATT	Megara, Exo Vrisi	37°59'58.3"N, 23°20'00.3"E	31.x.2021	1	306	OG, OI, WM, PO, EO, EV, MB, SM
ATT	Megara, Pachi	37°58'51.6"N, 23°21'12.6"E	4.vii.2021	1	63	WM, EV
ATT	Moschato	37°56'42.9"N, 23°40'49.6"E	v-viii.2021	1	84	OG, OI, WM, EV
ATT	Nea Peramos	38°00'04.3"N, 23°25'14.6"E	iv-xi.2021	9	1080	OG, OI, WM, PO, EO, EV, MB, OR, SM
ATT	Neos Kosmos, Fix	37°57'52.8"N, 23°43'39.3"E	28.viii.2021	1	9	EV
ATT	Neos Kosmos, Syngrou	37°57'43.1"N, 23°43'20.7"E	28.viii.2021	1	2	OG, WM, EV, SM
ATT	Perama, Centre	37°57'48.1"N, 23°34'31.2"E	iv-x.2021	4	425	OG, OI, WM, PO, EV, MB, OR, SM
ATT	Perama, Port	37°57'51.2"N, 23°33'31.0"E	v-x.2021	2	123	OG, OI, WM, PO, EV, MB, SM, SC
ATT	Piraeus, Port	37°56'43.9"N, 23°38'27.6"E	viii-x.2021	1	764	OG, OI, WM, PO, EO, EV, MB, OR, SM, SC
ATT	Piraeus, Arch. Museum	37°56'49.0"N, 23°39'02.6"E	28.viii.2021	1	60	EV
ATT	Piraeus, Korai Square	37°56'31.6"N, 23°38'50.1"E	viii-ix.2021	3	74	OG, WM, EV
ATT	Piraeus, Sfaktirias Square	37°57'07.9"N, 23°37'58.7"E	5.x.2021	1	15	OG, EV
ATT	Piraeus, Vourlon Square	37°56'59.0"N, 23°38"01.1"E	5.x.2021	2	7	EV
ATT	Renti	37°58'28.1"N, 23°40'02.8"E	25.ix.2021	1	17	OG, WM, EV, MB
ATT	Salamina, Agia Kyriaki	37°58'05.9"N, 23°30'08.4"E	v-viii.2021	2	353	OG, OI, WM, EO, EV, MB
ATT	Salamina, Ambelakia	37°56'54.1"N, 23°32'00.9"E	9.v.2021	2	15	OG, WM, EV
ATT	Salamina, Iliakti	37°57'25.8"N, 23°25'54.5"E	27.ix.2021	1	47	OG, EV
ATT	Salamina, Selinia	37°55'44.3"N, 23°32'06.0"E	iv-vi.2021	1	77	OG, OI, WM, EV, MB
ATT	Salamina, Sinikismos	37°57'37.5"N, 23°31'14.5"E	23.viii.2021	1	178	OG, WM, EV

Adm. division	Site	Coordinates	Date(s)	Number of crops	Number of figs	Species present
ATT	Tauros	37°57'37.1"N, 23°41'58.8"E	28.viii.2021	1	72	EV
CG	Agios Konstantinos	38°45'20.5"N, 22°53'46.1"E	2.x.2021	1	17	EV
Cr	Chania, Municipal Garden	35°30'42.1"N, 24°01'30.7"E	14. xi.2021	4	11	OG, OI, WM, PO, EV, MB, SM
Cr	Chania, Municipal Market	35°30'51.5"N, 24°01'14.8"E	14. xi.2021	9	23	OG, OI, WM, PO, EV, MB, SM
Cr	Chania, Souda	35°29'14.3"N, 24°04'37.0"E	14. xi.2021	1	117	OG, OI, WM, PO, EV, SM, SC
Cy	Antiparos, Chora	37°02'25.1"N, 25°04'51.5"E	18.ix.2021	1	36	OG, WM, PO, EV, SM
Cy	Kimolos, Psathi	36°47'14.4"N, 24°34'42.6"E	3.ix.2021	1	188	OG, OI, WM, PO, EV, MB,
Cy	Kithnos, Merichas	37°23'31.8"N, 24°23'51.4"E	27.vi.2021	1	26	OG, EV
Cy	Milos, Adamas	36°43'27.5"N, 24°26'37.4"E	4.ix.2021	1	183	OG, OI, WM, PO, EV, MB, OR, SM, SC
Cy	Milos Katifora	36°44'07.4"N, 24°26'30.9"E	5.ix.2021	1	134	OG, OI, WM, PO, EV, SM
Cy	Paros, Paroikia	37°05'07.3"N, 25°08'56.1"E	18.ix.2021	3	438	OG, OI, WM, EV, SM, SC
Cy	Sifnos, Artemonas	36°58'25.9"N, 24°43'24.1"E	viii.2021	1	52	EV
Do	Karpathos, Pigadia	35°30'29.5"N, 27°12'39.5"E	viii.2021	1	40	WM, EV
Do	Kos	36°53'36.2"N, 27°17'20.8"E	vi.2021	1	12	EV
Do	Rhodes, Agios Frangiskos	36°26'21.3"N, 28°13'28.9"E	viii.2021	1	29	EV
Do	Rhodes, Ethinkis Antistasis	36°26'00.3"N, 28°13'26.2"E	viii.2021	1	71	OG, OI, WM, MD, PO, PT, EO, EV, MB, SM, SC
Do	Rhodes, Rodiaki Epavli	36°26'52.6"N, 28°13'08.2"E	viii.2021	1	191	OG, OI, WM, PO, EV
Do	Rhodes, Rodini Park	36°25'37.2"N, 28°13'16.7"E	viii.2021	1	87	OG, WM, PO, EV
Do	Tilos	36°24'58.2"N, 27°23'06.8"E	vi.2021	5	355	OG, OI, WM, EV
Iis	Zakynthos Ag. Kirikos	37°47'15.1"N, 20°49'41.6"E	10.iv.2022	1	3	OG, EV
Iis	Zakynthos Argasi	37°45'54.6"N, 20°55'20.1"E	9.iv.2022	1	7	OG, WM
Iis	Zakynthos Chora	37°46'55.0"N, 20°53'50.0"E	10.iv.2022	3	26	OG, OI, WM
PEL	Agioi Theodoroi	37°55'33.6"N, 23°08'34.8"E	iii-ix.2021	4	148	OG, OI, WM, PO, EO, EV, MB, OR, SM, SC
PEL	Ermioni	37°23'08.2"N, 23°14'54.6"E	vi.2021	1	15	OG, WM, EV, SM
PEL	Loutraki, Park	37°58'25.1"N, 22°58'45.2"E	vi-ix.2021	2	100	OG, OI, WM, PO, EV
PEL	Loutraki, Spiritual Centre	37°58'36.4"N, 22°58'43.3"E	vi-ix.2021	2	80	OG, OI, WM, PO, EV, SM, SC
PEL	Korinthos Centre	37°56'23.7"N, 22°56'00.7"E	25.vii.2021	1	61	OI, WM, EV
PEL	Korinthos South Town	37°56'18.8"N, 22°56'59.0"E	25.vii.2021	1	16	WM, EV
PEL	Nafplio	37°33'59.9"N, 22°48'01.2"E	v-xi.2021	4	74	OG, OI, WM, PO, EO, EV, MB OR, SM
PEL	Patra	38°14'56.5"N, 21°44'06.1"E	8.iv.2022	1	32	OG, EV

Table 3. Number of occupied administrative divisions, year of first published record, total number of specimens and percentage for each fig wasp species recorded from Greece.

Species	Year of first record	Number of adm. divisions occupied	Total number of specimens	Percentage
Eupristina verticillata	2014	6	11537	53.76%
Eufroggattisca okinavensis	2023	2	82	0.003%
Meselatus bicolor	2014	5	1840	0.085%
Odontofroggatia galili	1989	7	3827	0.1783%
Odontofroggatia ishii	2014	5	984	0.045%
Odontofroggatia quinifuniculus	2023	1	4	0.0001%
Sycophila curta	2023	4	59	0.002%
Sycophila maculafacies	2014	4	619	0.028%
Ormyrus microcarpae	2023	3	239	0.011%
Micranisa degastris	2023	1	9	0.0004%
Philotrypesis okinavensis	2014	4	553	0.025%
Philotrypesis taiwanensis	2023	1	17	0.0007%
Walkerella microcarpae	2014	5	1687	0.078%

Recently, and increasing number of fig wasp species have been found outside their native range, while there is lack of knowledge regarding the extend of their distribution in their putative native ranges. These include *Acophila microcarpa* Chen, 1999 (UAE), *Eufroggattisca okinavensis* Ishii, 1934 (Cyprus), *Odontofroggatia corneri* Wiebes, 1980 (South Africa) and *Sycophila petiolata* Chen, 1999 (Cyprus) (van Noort and Rasplus 2010; van Noort et al. 2013; Demetriou et al. 2023). The application of molecular tools has proved to be crucial on the research of fig wasp species that are very closely related as shown in this study by the detection of the erroneous assignment of *P. okinavensis* specimens from Greece to *P. emeryi* (Wang et al. 2015a). *Philotrypesis emeryi* has been also reported from neighbouring Turkiye (Doganlar 2012). Nevertheless, given that only *P. okinavensis* occurs in Greece (and by extension into the SE Aegean, which is in close proximity with the neighbouring country) and Cyprus, records from Turkiye should be re-evaluated using both morphological and molecular tools in order to rule out possible misidentifications in Doganlar (2012). Future application of molecular tools alongside morphological examination of specimens is expected to reveal further cryptic or new species and, as such, the number of alien fig wasps could further rise (Sun et al. 2011; Wang et al. 2015a; J-Y Rasplus, pers. comm.). To support this claim, in the phylogenetic analysis of *Philotrypesis* performed in this study, already a number of undescribed *Philotrypesis* lineages have been indicated (Fig. 2).

The presence of the fig wasp species in Greece is likely to be the result of recent introductions. This can be supported by the number of species recorded in the area (Dodecanese Islands) where three different sampling attempts were made at different time intervals (Wang et al. 2015a). Starting with the initial detection of *Odontofroggatia galili* from the island of Symi (Compton 1989), samples from the islands of Rhodes and Symi twenty-five years later increased the number of fig wasp species to seven (Wang et al. 2015a), eventually rising to thirteen with the addition of six species in the present study. Interestingly, most of these species (ten out of thirteen) are present in the Dodecanese Islands. This trend seems to follow globalisation, international trade and the translocation of exotic plants around the world (Mack et al. 2000; Wang et al. 2015a). Nevertheless, the possibility that

these species could have been present from the earliest introductions of *F. microcarpa* to Greece cannot be completely ruled out, given this is the first extensive sampling effort carried out on a national level. Wang et al. (2015a) discussed how the secondary spread of different fig wasp species throughout the Mediterranean could have already taken place or is likely to take place in the future, either naturally or via human mediation. Some of the fig wasps associated with *F. microcarpa* could have reached the country from already invaded territories, such as Cyprus and Turkiye, where a significant number of species are present (Doganlar 2012; Wang et al. 2015a; Demetriou et al. 2023), with the assistance of air currents (van Noort and Rasplus 2010). It is possible that some of these species have managed to spread throughout the Aegean in the same manner. After all, air-borne movement by fig wasps has already been recorded to exceed distances of up to 160 km in the Namib Desert (Ahmed et al. 2009).

Invasiveness and impact of *Ficus microcarpa*

As mentioned above, *F. microcarpa* is an ornamental plant with a wide distribution beyond its natural range. Followed and assisted by its pollinator *E. verticillata*, it has managed to establish and even become invasive in some areas (Malta, Hawaii and many southern parts of the USA) (Wang et al. 2015b; Compton et al. 2018). In Greece, cases of germination and development of small seedlings have already been reported on the medieval walls of Rhodes (Galanos 2015). Similar cases of seedlings developing on walls were observed in the port of Piraeus near fig trees (Fig. 3a, Table 4). Due to its resistance to salinity, a well-developed *F. microcarpa* shrub was also observed on the dock of Agios Nikolaos (Crete) with its base standing just a few centimetres above sea level (Fig. 3b). These observations reinforce our concerns that *F. microcarpa* may eventually manage to escape urban habitats into semi-natural or even natural habitats, affecting native plant diversity. This is of particular importance in the Dodecanese and other Aegean Islands, where the establishment of an alien plant may disproportionally affect native island flora (Ramírez and Montero 1988; Starr et al. 2003; Reaser et al. 2007; Hulme et al. 2008; Russell et al. 2017). The socioeconomic and human-health risks related to the ripe fallen figs are also worth discussing. Ripe figs falling to the ground have been mentioned to form a slippery amorphous mass, which can not only attract harmful insects (i.e. flies), but also endanger pedestrians or damage property such as parked cars (Fig. 3c, d) (Ramírez and Montero 1988; Beardsley 1998; Tsintides et al. 2002; Demetriou et al. 2023).

Table 4. List of sites in which seedlings of *F. microcarpa* were observed, in Greece.

Administrative region/locality	Coordinates	Date	Habitat	Type of infrastructure seedlings were found on	Reference
Dodecanese/Rhodos town/Rodiaki epavli	36°26'53"N, 28°13'10"E	21.xi.2014	Urbanized	In crevices of walls	Galanos (2015)
Dodecanese/Rhodos town	36°26'23"N, 28°13'25"E	11.i.2015	Urbanized	Medieval castle walls	Galanos (2015)
Dodecanese/Rhodos town	36°26'46"N, 28°13'41"E	18.i.2015	Urbanized	Medieval castle walls	Galanos (2015)
Attica/Piraeus port	37°56'44.2"N, 23°38'27.9"E	25.vi.2021	Urbanized	Marble wall	Present study
Crete/Agios Nikolaos town	35°11'25.3"N, 25°43'05.1"E	24.viii.2022	Urbanized	Sea wall	Present study
Peloponnese/Xylokastro	38°04'40.8"N, 22°37'40.8"E	8.x.2022	Urbanized	Sidewalk	Present study
Peloponnese/Nafplio	37°33'57.0"N, 22°47'58.5"E	19.xi.2023	Urbanized	On *Phoenix* sp.	Present study

Figure 3. **a** *Ficus microcarpa* small tree, in Agrios Nikolaos port, Crete **b** *F. microcarpa* seedling in Piraeus port **c, d** Ripe figs under *F. microcarpa* trees in Heraklion, Crete.

Aiming to mitigate the impact and the possibility of *F. microcarpa* becoming invasive, Wang et al. (2015b) investigated the use of gall-inducing fig wasps as biological control agents against the pollinator *E. verticillata*. While *O. galili* is the most widespread fig wasp species after the pollinator in its invaded areas, its role on the reduction of pollination was not deemed significant (Wang et al. 2015b). In contrast, *M. bicolor* creates galls that nearly always prevent pollination and seed production (Wang et al. 2015b). While this species was only known from the Dodecanese Islands at the time, Demetriou et al. (2023), as well as the present study, show that it has a remarkable distribution in both Greece and Cyprus. The species' extended distribution could enhance efforts to study its potential in the biological control of its host-plant, although the discovery of its parasitoid *O. microcarpae* could be a hindering factor for such schemes (Koutsoukos et al. 2024). Nevertheless, given the large number of fig wasp species associated with *F. microcarpa*, newly-arrived species may prove equally effective or better than *M. bicolor*.

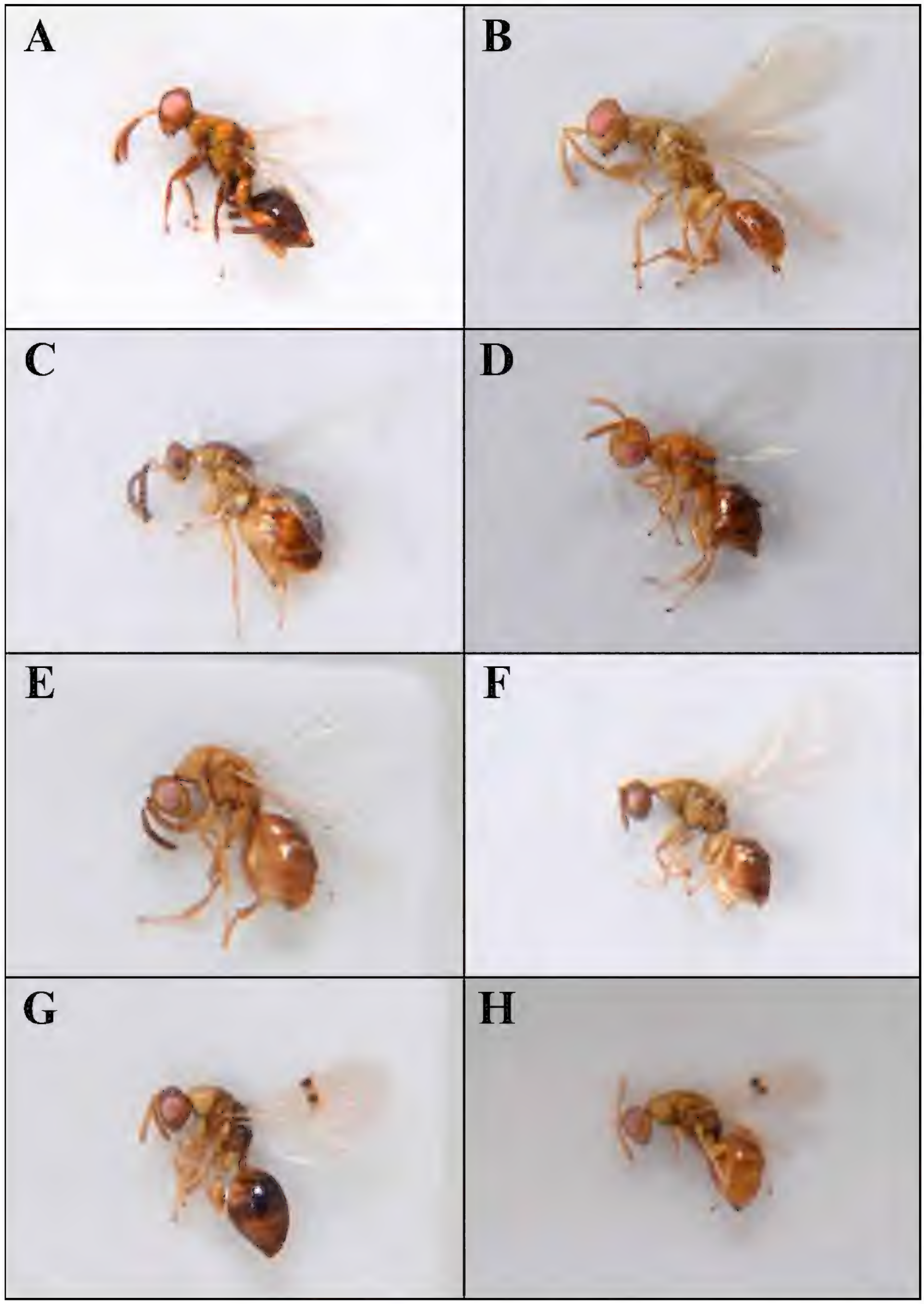

Figure 4. Species reared from *F. microcarpa* figs during this study **A, B** *Eufroggattisca okinavensis*, female and male **C** *Odontofroggatia galili*, female **D** *Meselatus bicolor*, female **E** *Odontofroggatia ishii*, female **F** *Odontofroggatia quinifuniculus*, female **G** *Sycophila maculafacies*, female **H** *Sycophila curta*, female.

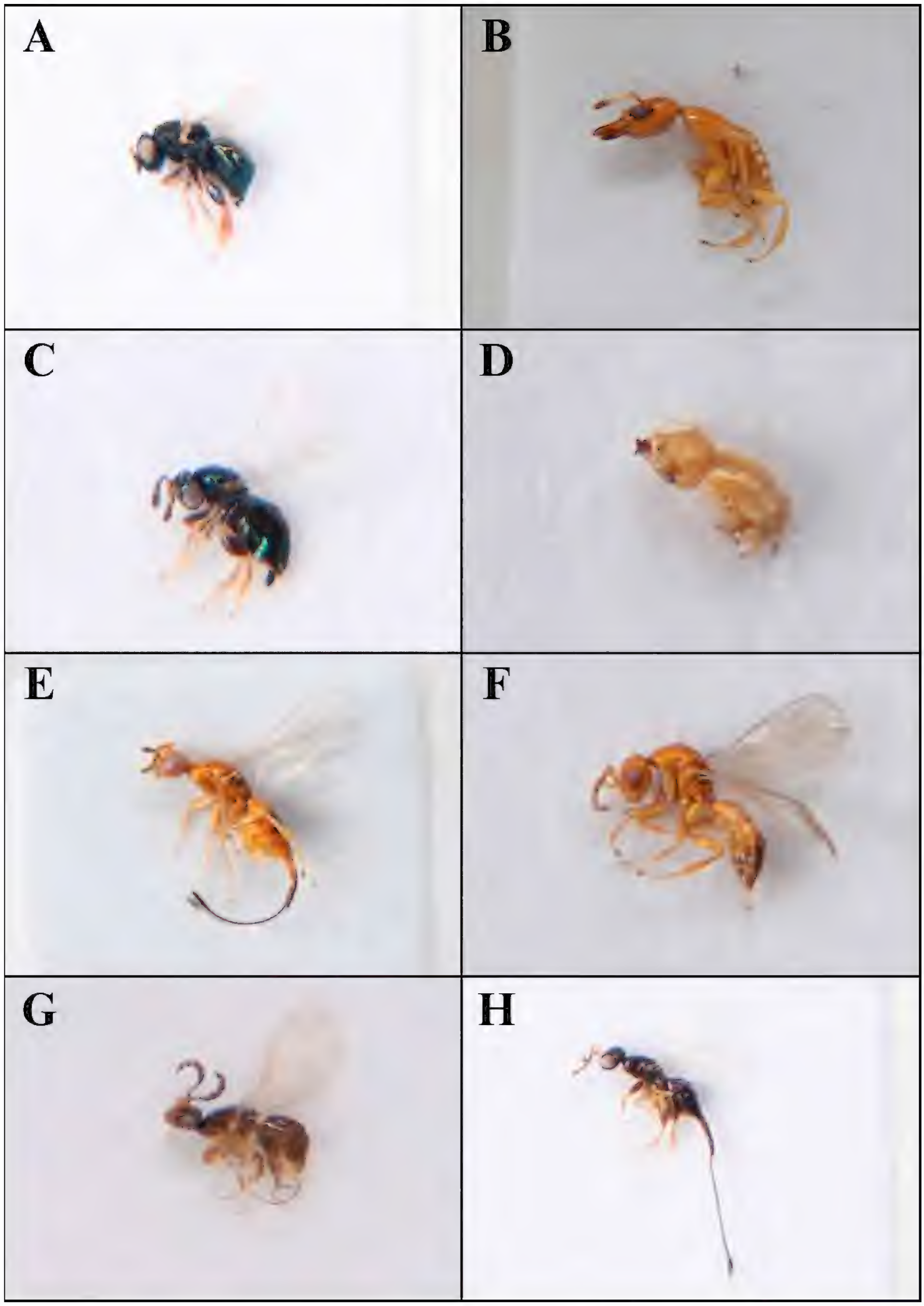

Figure 5. Species reared from F. microcarpa figs during this study **A, B** *Walkerella microcarpae*, female and male **C, D** *Micranisa degastris* **E, F** *Philotrypesis okinavensis*, female, male **G** *Eupristina verticillata* **H** *Philotrypesis taiwanensis*, female.

As remarked above, *M. bicolor* is the NPFW with the highest impact on both the pollinator and the tree, even though it does not have the same abundance and prevalence as *O. galili*. *Odontofroggatia* species, *W. microcarpae*, *P. taiwanensis* and *M. degastris* can also negatively affect *F. microcarpa* by interacting with the pollinator, although insignificantly, when compared with *M. bicolor*. Nevertheless, the widespread and high abundance of species, such as *O. galili* and *W. microcarpae*, could be auxiliary to efforts for limiting *E. verticillata*. Other NPFW species present in Greece include parasitoids that attack the aforementioned species that are competitive to the pollinator and, as such, are beneficiary to *E. verticillata* and the reproduction and expansion of *F. microcarpa*. These include both *Sycophila* species (parasitoids attacking *Odontofroggatia* spp.) and most notably the newly-discovered *O. microcarpae* that attacks *M. bicolor*. Species with an ambiguous role include *P. okinavensis*, which parasitises both *W. microcarpae* and the pollinator (Compton et al. 2018) and *E. okinavensis*, which is found in *M. bicolor* galls, although whether it is a parasitoid or an inquiline is yet unclear.

Given the widest distribution (82.7% prevalence) and highest percentage (53.76%) amongst all species collected, *E. verticillata* will continue to assist its host-plant to reproduce. As such, it is distinctly possible that cases of germination and development of seedlings will multiply and all adverse socioeconomic impacts associated with *F. microcarpa* will persist. Taking into account the rich fig wasp fauna associated with *F. microcarpa* in Greece, future research could shed further light on the complex trophic webs within figs and how these are affecting *E. verticillata*. This could possibly serve as the baseline for monitoring schemes in order to prevent *F. microcarpa* establishing in native habitats and becoming invasive.

Conclusions

A total of 13 alien fig wasp species have been recorded from Greece, with their number almost doubling since previous studies (Wang 2014; Wang et al. 2015a; Wang et al. 2015b). Nevertheless, as new alien species are constantly being discovered outside their native range, including species associated with *Ficus* spp. (Beardsley and Rasplus 2001; Koutsoukos et al. 2024), their numbers are predicted to increase even further. These species are mostly represented in the Aegean Islands, where their host plant is more common due to warmer climatic conditions.

As earlier discussed, new records are hypothesised to represent newly-introduced species; nevertheless, this statement is not definitive. As such, wider-scale sampling is necessary to assess the biodiversity of fig wasps on a national level. Furthermore, the application of molecular tools is planned to investigate gene flow and the genetic diversity, especially between island populations. As new additions to the checklist are anticipated, it is important to investigate the introduction pathways and means of spread of alien fig wasps, as well as their interplay with *F. microcarpa*, ensuring the plant will not manage to escape cultivation.

The reported displacement of native flora by *F. microcarpa* in invaded parts of the world is problematic (Wang et al. 2015a). Seedlings both in Greece and Cyprus have been observed in urban habitats, with their spread being assisted by pollination of the figs by *E. verticillata* and the subsequent ingestion of ripe fruits and excretion of the seeds by birds (Galanos 2015; Demetriou et al. 2023; present study). In Cyprus, seedlings in the Limassol city centre were found in areas with sufficient irrigation (under rainspouts) and covered in bird droppings.

This shows that not all available natural habitats could be potentially colonised by *F. microcarpa*, especially in the arid Mediterranean islands. Nevertheless, habitats with sufficient moisture or water content visited by birds, such as riparian vegetation and other inland waterbodies, already hosting a large number of naturalised alien plants (Arianoutsou et al. 2010), could be monitored in the future.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

DNA barcoding specimen codes, accession numbers and specimen details for representatives of the genus *Philotrypesis*

Authors: Evangelos Koutsoukos

Data type: xlsx

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Supplementary material 2

Detailed number of specimens per species from each sampled locality

Authors: Evangelos Koutsoukos

Data type: xlsx

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Supplementary material 3

Presence and prevalence of fig wasp species

Authors: Evangelos Koutsoukos

Data type: xlsx

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